

REPRODUCTION AND MOVEMENTS OF MOUNTAIN PLOVERS BREEDING IN COLORADO

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ABSTRACT.—North American populations of Mountain Plovers (*Charadrius montanus*) have declined 63% since 1966. Using radiotelemetry, we monitored plover nesting and brood rearing during the 1993 and 1994 breeding seasons in Weld County, Colorado. Our objectives were to extend preliminary breeding studies of 1992 (Miller and Knopf 1993) and to determine the minimum area required for successful reproduction by this species. Plovers began arriving on the breeding grounds in mid-March. Due to a high incidence of predation, eggs hatched in only nine of 34 (26%) nests in 1993 and in 20 of 54 (37%) nests in 1994. Daily survival rates of chicks were 0.957 (442 telemetry days, 44 chicks) and 0.951 (610 telemetry days, 42 chicks) each year, respectively. Plover broods moved an average 337 ± 46.5 m/day ($N = 30$) and 298 ± 41.9 m/day ($N = 14$) in 1993 and 1994 ($t = 1.10$, $P = 0.27$), respectively. Plovers that raised chicks to fledging used between 28 and 91 ha, averaging 56.6 ± 21.5 ha. Daily movement rates ($t = 0.7$, $P = 0.48$) and total area used ($t = 1.4$, $P = 0.17$) were similar between broods where \geq one chick fledged and broods from which no chicks fledged. Success of plovers in raising chicks appeared related either to overall fox activity in the area or to how effectively the adult detected and distracted foxes. Most plovers left the breeding grounds in mid-to-late July, four months after arrival. Population declines of Mountain Plovers appear independent of any recent landscape fragmentation within this breeding stronghold of the species. Received 10 May 1995, accepted 1 Oct. 1995.

North American Mountain Plover (*Charadrius montanus*) populations declined 63% between 1966 and 1991 (Knopf 1994) and the decline has continued through 1993 (Knopf, in press). This species nests across the western Great Plains and eastern Colorado Plateau region, with the breeding stronghold being in Weld County, Colorado (Graul and Webster 1976). Mountain Plover nests are located in microsites of native short-grass prairie dominated by blue grama (*Bouteloua gracilis*) with 30% or more of the area being bare ground (Knopf and Miller 1994; Knopf and Rupert 1996). A female plover lays a clutch for the male to incubate then a second clutch for herself (Graul 1973). The precocial chicks receive uniparental care and move up to 800 m from the nest shortly after hatching (Graul 1975). Brood-rearing habitat is described as areas with forbs or objects such as fence posts where chicks can find shade to avoid mid-day heat (Graul 1975).

In this study, we used radiotelemetry to monitor movements and determine the area requirements of Mountain Plovers during the breeding season. We also provide information on nest success and chick survival to supplement preliminary findings of Miller and Knopf (1993) in 1992.

We interpret our findings relative to conservation of this rapidly declining species.

METHODS

We studied Mountain Plovers during the 1993 and 1994 breeding seasons on the Pawnee National Grassland (PNG), a 781-km² shortgrass prairie. Graul (1973) summarized the physiography, vegetation, and climate of this region. We concentrated our study on three grazing allotments (Keota, Keota Steer, and Owens) in the vicinity of Keota, Colorado, and on three other allotments (Reno, Sand, and Wildhorse) northwest of Briggsdale, Colorado.

Once a nest was located, we monitored the progression of incubation (29 days) by egg flotation every 3–5 days. During nest monitoring, we drove a vehicle near the nest and, remaining in the vehicle, reached down to remove an egg to avoid spreading human scent in the vicinity. Within 2–4 days before hatching we captured adult birds on nests with a fishing line snare or swing-door box trap made of wire mesh. In 1993, some juveniles from unknown nests were captured by hand and aged per Miller and Knopf (1993) to supplement survival rate data on older chicks.

All birds were banded with a U.S. Fish and Wildlife Service numbered metal band on one leg and colored plastic bands on the other. Plovers ($N = 43$) were fitted with 1.5–3.0 g radio transmitters with 15 cm antennae (Holohil Ltd., Woodlawn, Ontario, Canada, and Advanced Telemetry Systems, Isanti, Minnesota. Mention of commercial products does not constitute endorsement by the U.S. Government). The transmitter was affixed by applying a light coating of waterproof epoxy adhesive (Titan Corp., Lynnwood, Washington) and sliding it under the upper back feathers. Care was taken not to expose the skin to the epoxy. The transmitter was not visible on the birds and the whip antenna was difficult to see even with binoculars at close (<20 m) distances. Transmitter life was about 90 days, and transmitters remained attached to adult birds until the prebasic molt. Birds were not handled after initial transmitter attachment.

All chicks in monitored nests were color banded on the day of hatching, then never rehandled. We subsequently located broods almost daily at distances up to 1000 m with a TRX-1000 Wildlife Materials Inc. (Carbondale, Illinois) receiver and a hand-held, three-element Yagi antenna. All relocations were from a vehicle, again to avoid spreading human scent. Specific locations of plovers were recorded using the Magellan NAV 5000 Global Positioning System [Magellan Systems Corporation, San Dimas, California]. Position readings were recorded to the nearest hundredth of a minute and only if a satellite geometric quotient registered ≥ 7 on a scale of 1–9. Based upon readings at a known (surveyed) benchmark, accuracy of our specific instrument was calculated at 7.2 ± 1.4 ($\bar{x} \pm SD$) m latitude and 8.4 ± 1.6 m longitude for an area error of ± 60.6 m².

The area used by broods was estimated by superimposing a grid over a map of the study area and counting the number of new cells (10×10 m) visited over time. This is an adaptation of the grid-cell home range estimation method first proposed by Siniff and Tester (1965). Whereas discontinuous telemetry data often result in successive locations being several cells apart, we conservatively assumed that birds traveled in a straight line between locations. Thus, area-of-use descriptions are considered to be the minimum (vs actual) area requirements for raising a brood.

RESULTS

Egg/chick survival.—Plovers were first observed on the PNG on 17 March 1993 and 21 March 1994, although the exact date of the first bird

TABLE 1
PRODUCTIVITY AND CHICK SURVIVAL RATES OF MOUNTAIN PLOVERS ON THE PAWNEE
NATIONAL GRASSLAND, WELD COUNTY, COLORADO, 1992–1994

Year	No. nests	Nest success (%)	\bar{x} No./Successful nest			Daily survival rate
			Eggs hatched	Chicks fledged	Chicks migrated ^a	
1992 ^b	14	50	2.6	1.21	0.74	0.977
1993	34	26	2.4	0.26	0.22	0.957 ^c
1994	54	37	2.6	0.35	0.17	0.951 ^d

^a Calculated from average of 18 days that chicks remained on breeding grounds after fledging (Miller and Knopf 1993).

^b Data from Miller and Knopf (1993).

^c Based on 442 telemetry days, 44 chicks.

^d Based on 610 telemetry days, 42 chicks.

arriving may have been a day or two earlier. We monitored 34 nests in 1993 and 54 nests in 1994. Three clutches were abandoned each year. In 1993, two clutches were abandoned after being partially predated. The other clutch was abandoned after it had been flooded from 4 to 6 June and then incubated again from 7 to 20 June. In 1994, two clutches were abandoned for unknown reasons. One other was abandoned after being incubated two weeks beyond normal hatching time. Adult plovers from three of the six nesting efforts stayed in the nest area until migrating, whereas the other three left the area within 48 hours and could not be relocated.

Predation rates on both eggs and chicks were high (see Miller and Knopf [1993] for a list of potential predators), and egg and chick survival were low (Table 1). Survival probabilities of the 1994 chicks partitioned into 10-day intervals (day 1–10 = 0.935, 11–20 = 0.957, 21–30 = 0.970, and 31–40 = 0.971) indicate that survival increased with age of the chick. Generally, daily survival rates were only slightly lower than reported for 1992 (Miller and Knopf 1993). However, the lower daily rates resulted in a drastic decline in the number of chicks produced per nesting effort if projected to the time when fledged chicks left the breeding area.

Movement patterns.—We captured and placed transmitters on 17 and 26 adult plovers with broods in 1993 and 1994, respectively. Each brood was tracked until either all members of the brood were killed by a predator or fledged chicks left the nest vicinity. Of adults fitted with transmitters, we obtained prolonged movement and area-of-use data on seven and 14 broods in 1993 and 1994, respectively. An additional 26 chicks were aged and fitted with transmitters in 1993, of which 23 provided usable information. Thus, data were obtained on 30 broods in 1993 and

14 broods in 1994. The average duration of radio-tracking was 10.3 ± 5.2 and 22.9 ± 13.4 days for each brood in 1993 and 1994, respectively.

Based upon 290 telemetry days, plover broods moved an average of 337 ± 46.5 m/day in 1993 (range 61 to 600 m). The 320 telemetry days in 1994 indicated an average move of 298 ± 41.9 m/day (range 85 to 651 m). Distances moved were similar ($t = 1.10$, $P = 0.27$, 608 df) between years. Of the 42 broods, 38 moved 100–500 m/day. Of the remaining four broods, two were monitored for only five days and moved <100 m/day. Two others, monitored four days and 13 days, moved 1000 and 1085 m/day, respectively.

Most losses of chicks were to swift foxes (*Vulpes velox*). Average daily movements were similar ($t = 0.7$, $P = 0.48$, $df = 40$) among broods in which all chicks were killed by predators (400 ± 313 m, $N = 15$) and broods where chicks fledged (340 ± 226 m, $N = 27$). The total distances moved during the first 10 days after hatching of eggs (when predation rates were highest) were also similar ($t = 0.50$, $P = 0.62$, $df = 14$) between broods in which all chicks were lost and broods where chicks fledged.

Brood-rearing area.—Due to the high rates of predation and some transmitters on older chicks becoming dislodged, we were only able to track six broods from hatching to fledging. The total minimum area used by those six broods ranged from 28 ha to 91 ha and averaged 56.6 ± 21.5 ha. As suspected from the movement data, the average area used on a daily basis by broods where chicks fledged (2.5 ± 1.6 ha, $N = 27$) vs broods that lost all chicks to predators (3.4 ± 2.4 ha, $N = 15$) were similar ($t = 1.4$, $P = 0.17$, $df = 40$).

Timing of departure.—At least two adults renested after losing a clutch or brood early in the breeding season (May, early June). One adult whose chicks hatched on 21 May 1993 was located on a second nest 140 m away on 21 June. The transmitter had failed, so knowledge of the fate of the first brood of three chicks is not certain. This bird abandoned its second clutch after it was partially depredated; it remained in the vicinity with other plovers until 14 July when it left the area, returned 26–29 July, then left the area for the season.

This example illustrates the general pattern of flocking and departure from the breeding grounds. A few adult plovers began congregating in flocks in mid-June each year. Fledglings started to appear in these flocks in July. Many adults also were undergoing a prebasic molt at this time, precipitating an increased rate of transmitter loss. Plovers with transmitters began leaving the study areas gradually after mid-June, but a major exodus of plovers occurred mid-late July. Seventeen plovers in 1993 and eight plovers in 1994 which were being located daily were known to have

left the study area between 14 July and 3 August. In 1993, an aerial survey of Weld County from 3 to 9 August confirmed that not one of 17 transmittered birds remained in the vicinity. The few adults (transmittered and untransmittered) that we could find in early August of 1993 all had large chicks incapable of flight.

DISCUSSION

Productivity.—Miller and Knopf (1993) reported that adult survival and productivity on the PNG were similar to historical studies. We recently documented that survival rates of birds wintering in California are also high (Knopf and Rupert 1995). In this study, we recorded daily survival rates of chicks in 1993 and 1994 similar to those reported for 1992. The more intensive efforts described here detected an increasing probability of survival with age of the chick, as reported by Graul (1975). Thus, the 1992 daily survival rate (0.977) was inflated slightly by a high incidence of older chicks being transmittered that year.

An unknown percentage of female plovers lay two clutches, the male incubates the first as the female lays a second clutch for herself (Graul 1973). The incidence of male-incubated clutches may increase with food abundance (Graul 1976). Thus, whereas 0.26 and 0.35 chicks fledged per nest compares poorly with fledging rates of some other North American plovers (Page et al. 1983, Haig and Oring 1988, Prindiville Gaines and Ryan 1988), the actual productivity per pair may be up to twice that value in a given year.

The number of eggs hatched per clutch has remained stable when compared to studies conducted 10 (McCaffery et al. 1984) and 25 (Graul 1975) years earlier. Most reproductive losses were due to fox predation. We believe that the greater losses of nests and chicks to predators in 1993 and 1994 compared to 1992 were attributable indirectly to reduced food resources. Mountain Plover reproductive efforts (Graul 1976), as those of other grassland birds (George et al. 1992), are less successful in years of drought. The two seasons of this study were drought years on the PNG. Grasshoppers are a major food item of both plovers and foxes, and their populations were very low both years. Low grasshopper populations would increase the time spent foraging for both species, thus increasing the probability of eggs and chicks being detected by foxes.

Movement patterns.—Reproductive success of many birds appears to be a tradeoff between acquiring food and risking predation (Martin 1992). From an evolutionary perspective, numerous traits of Mountain Plovers may reduce detection by predators, including the cryptic coloration of chicks and crypsis to avoid detection (Sordahl 1991), two clutches incubated separately by the two adults (Graul 1973), shell removal at hatch-

ing (Graul 1975), rapid movement of chicks away from the nest (Graul 1975), predator distraction displays by adults (McCaffery et al. 1984), and the ability of chicks to fly at only 70% of adult body weight (Miller and Knopf 1993).

Mountain Plovers led hatchlings away from the nest as soon as they were dry. We regularly tracked the directional movement of a brood up to 2 km within two or three days of hatching. Many plovers moved broods to areas of disturbed prairie (Knopf and Rupert 1996) and then remained in those general areas. In contemporary prairie landscapes, such disturbances are either areas frequented for watering and loafing by cattle or fallow agricultural fields. After the initial move, many broods remained in the vicinity of these areas where chicks foraged on small insects.

Area requirements.—This study was precipitated by the conservation need for information on the minimum area necessary for plovers to raise chicks. The minimum area within which a brood was raised was 28 ha. Plovers raised chicks in broadly overlapping areas, with two or three broods sometimes occurring in a general vicinity (such as around a cattle watering tank). Thus, the potential exists for a suitable area to meet the needs for more than one bird to raise chicks successfully.

The movement rates and area-of-use by plovers that successfully raised their chicks to fledge did not differ from those of plovers that lost the entire brood. Swift foxes were often seen hunting during daylight hours (especially after mid-June as pups began eating prey) in addition to night foraging. The eventual success of a plover in raising its chicks appeared to be the result of either the overall fox activity in the immediate area being used by the brood or the effectiveness of the adult plover in detecting and distracting a fox.

Departure from breeding grounds.—Most Mountain Plovers that bred in Weld County left by 1 August each year. Occasional flocks of plovers were seen after early August, with the latest being on 8 October 1993. We assumed the later flocks were of birds moving south from more northerly nesting areas. The first plovers arrive on California wintering grounds in mid-October. The prolonged period of migration to the wintering areas is in sharp contrast to the apparently direct, nonstop flight from California back to Colorado in March (Knopf and Rupert 1995). Plovers spend approximately four months on their Colorado breeding grounds, five months on the California wintering grounds, and three months moving from the former to the latter.

CONCLUSIONS

Miller and Knopf (1993) concluded that recent population declines of Mountain Plovers can be attributed either to long-term declines in repro-

ductive success or to phenomena occurring at nonbreeding areas. The comparatively lower survival rates of chicks observed in 1993 and 1994 support that preliminary conclusion. Although swift fox densities seem high on the PNG, the fox is only locally distributed within the breeding range of the plover. We would not expect, for example, such a high rate of predation in Phillips County, Montana (the second major breeding locale) due to the absence of foxes in that state.

The shortgrass prairie, like many native vegetative associations, has become highly fragmented in the last century. The PNG is no exception, with 781 km² occurring in 130 parcels ranging from 16 to 23,895 ha (B. Ladd, pers. commun.). Although some of the smaller PNG parcels are <28 ha, the minimum area required for brood rearing, all are contiguous to private lands that are likewise managed as rangelands. We feel that these private lands also provide suitable Mountain Plover habitat. Thus, we conclude that virtually all relatively flat, grazed shortgrass prairie parcels provide potential habitats for plovers on the PNG. The current decline of the North American Mountain Plover population appears independent of recent fragmentation of landscapes within the native shortgrass prairie of northeastern Colorado, the breeding stronghold (Graul and Webster 1976) of the species.

ACKNOWLEDGMENTS

We thank the U.S. Forest Service, for financial assistance, and personnel of the Rocky Mountain Region, Arapaho-Roosevelt National Forest, and the Pawnee National Grassland District for technical assistance. We are especially grateful to Larry Mullen for administrative support. The Colorado Division of Wildlife conducted aerial reconnaissance, and we specifically thank Jim Dennis for his efforts. Susan Skagen and Tex A. Sordahl provided helpful comments on the manuscript. Clif Knopf provided assistance in the field.

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